

Chimpanzee Variation Facilitates the Interpretation of the Incisive Suture Closure in South African Plio-Pleistocene Hominids

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KEY WORDS *Australopithecus; Paranthropus; early Homo; South Africa; Pan; sutura incisiva; Stw 53*

ABSTRACT For a better understanding of early hominid growth patterns, we need to compare skeletal maturation among humans and chimpanzees. This study provides new data on variation of the incisive suture closure in extant species to facilitate the understanding of growth patterns among South African Plio-Pleistocene hominids. The complete anterior closure of the incisive suture occurs early during human life, mostly before birth. In contrast, in chimpanzees a complete anterior closure occurs mostly after the eruption of either the first permanent molars (pygmy chimpanzees) or the third molars (common chimpanzees). The first aim of this study is to test whether the patterns of closure of both the anterior and palatal components of the incisive suture in chimpanzees accurately mirror their polytypism by investigating 720 museum specimens of known geographical origin. Then we use the data gleaned from the incisive suture closure in chimpanzees to determine whether there are different growth patterns among South African Plio-Pleistocene hominids and to interpret them.

Results about the pattern of incisive suture closure are consistent with the differences among chimpanzees as revealed by molecular data. Thus, the variation in chimpanzee patterns of incisive suture closure facilitates the interpretation of morphology in South African fossil hominids. In *Australopithecus (Paranthropus) robustus* as compared to *Australopithecus africanus*, the complete anterior closure and, probably, the complete palatal closure of the incisive suture occurs during early life in the same way as they occur in humans. Moreover, the closure pattern observed on Stw 53, a supposed early *Homo* from Sterkfontein Member 5, is similar to that seen in *A. africanus* and in chimpanzees. Thus, with respect to the anterior component of the incisive suture, *A. africanus* and Stw 53 retain the primitive feature for which *A. (P.) robustus* and *Homo* share the derived character state. Finally, it is worth noting that the Taung child does not show the robust condition. *Am J Phys Anthropol* 105:121-135, 1998. © 1998 Wiley-Liss, Inc.

Exploring the developmental history of early hominids is a puzzling and debated issue in human evolution. The patterns of somatic growth have been interpreted by examining the rate and pattern of dental development (Mann, 1975; Smith, 1986, 1992; Beynon and Dean, 1988; Bromage, 1987; Mann et al., 1990; Conroy and Kuyken-

dall, 1995; Anemone et al., 1996). Major distinctions in pattern and timing of dental

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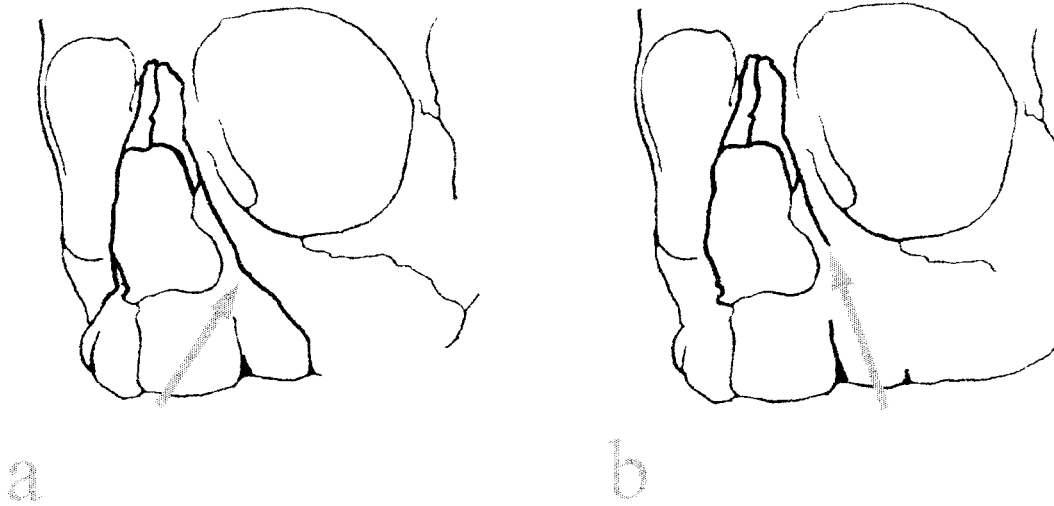


Fig. 1. The anterior component of the incisive suture (a) completely open in a chimpanzee foetus and (b) partially closed in a human foetus.

development have been found between humans and chimpanzees and then considered as useful landmarks to explore the developmental history of early hominids. However, for a better understanding of early hominid patterns of growth, we also need to compare skeletal maturation among humans and their closest biological relatives, chimpanzees. This study provides new data on variation of the incisive suture closure in humans and chimpanzees to facilitate the understanding of growth patterns among South African Plio-Pleistocene hominids.

The incisive suture (*sutura incisiva*) represents the contact area between the maxillary and the incisive bones. The incisive bone (*os incisivum*) is also called premaxillary bone, but the former name follows the International Code for Nomenclature (Sobotta, 1977). In this paper, I consider both facial and palatal components of the incisive suture. Usually, in chimpanzees the anterior component of the incisive suture extends, superiorly, for a small distance, between the nasal bone and the maxilla (Fig. 1). However, sometimes it may fail to reach as far upward as the nasal bone. The palatal component of the incisive suture extends, medially, from the lower aperture of the incisive canal (*canalis incisivus*) to, laterally, the interalveolar septum located between the

lateral incisor and the canine (Fig. 2). In humans, the closure of the palatal component of the incisive suture occurs at variable times after birth. It is generally admitted that, early in fetal growth, the incisive and maxillary bones represent two distinct entities, the contact area being a growth site. However, opinions diverge concerning the embryology of the incisive bone and its anterior relationship to the maxillary bone. Some authors claim that the incisive and maxillary bones unite by fusion at the ectofacial surface during the sixth to ninth week of embryonic life (Chase, 1942; Noback and Moss, 1953). Other authors hold that bone from the maxillary ossification center spreads anterior to the incisive bone between 12 and 16 weeks of fetal age (Callender, 1869; Vallois and Cadenat, 1924; Ashley-Montagu, 1935; Wood Jones, 1947; Woo, 1949). Kraus and Decker (1960) find that both fusion and overgrowth occur but not as described in the literature. In contrast, Wood et al. (1967) suggest that the incisive bone, in its alveolar region, may never have a truly separate existence in the human skull. However, in humans exceeding 6 years of age, the anterior component of the incisive suture is never observed (Ashley-Montagu, 1935).

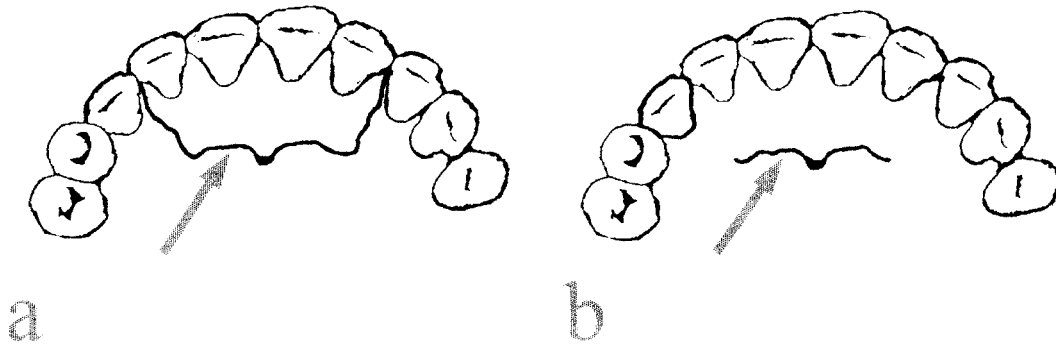


Fig. 2. The palatal component of the incisive suture (a) completely open and (b) partially closed.

In chimpanzees and, to a greater extent, in gorillas, the incisive bone loses its independence by a process of simple interstitial union across the incisive suture. The incisive suture tends to close later in species with prognathous faces than in those with more orthognathous faces (Krogman, 1930; Braga, 1995). Mooney and Siegel (1991:452–453) find a “patent facial component of the premaxillary-maxillary suture” in males and “a greater than 50% fused facial premaxillary-maxillary suture” in females. However, the observation of a complete patent anterior component of the incisive suture in the common chimpanzee as reported by Mooney and Siegel (1991) is highly questionable. Simpson and McCollum (1993) stress this point and mention three studies to support their view (Krogman, 1930; Ashley-Montagu, 1935; Schultz, 1948). My observations completely subscribe with Simpson and McCollum’s view. In a previous survey to determine anterior closure of the incisive suture in very young chimpanzees (Braga, 1995), which included 65 specimens either with exclusively deciduous teeth or with no permanent teeth in occlusion, a completely patent suture was never seen.

To sum up, two distinct closure patterns of the incisive suture are represented either by humans or by common chimpanzees (*Pan troglodytes*). In humans, the complete anterior closure of the incisive suture occurs very early during life (mostly during fetal life or, in rare cases, for its upper part, before 6 years of age). In common chimpanzees, the anterior closure of the incisive suture progresses with age but is mostly not com-

pleted until just after the third molars erupt. However, an important limitation to discuss the significance of the incisive suture closure in Plio-Pleistocene hominids is the lack of comparative data for pygmy chimpanzees (*Pan paniscus*).

GOALS OF THIS STUDY

The first aim of this study is to document the closure patterns of both anterior and palatal components of the incisive suture in pygmy and common chimpanzees by examining a sample of 169 and 551 specimens, respectively. Next, I consider whether the incisive suture closure accurately mirrors the chimpanzee polytypism by testing whether geographical variation (i.e., differences among interbreeding local populations to differences between subspecies) is important and by testing whether differences between species are significant. Finally, I use the data gleaned from chimpanzees to provide new insights about the incisive suture closure in South African Plio-Pleistocene hominids.

MATERIAL AND METHODS

The anatomical terminology used here follows that of the International Code for Nomenclature (Sobotta, 1977). All fossil hominids were examined with a low-power binocular microscope. Both anterior and palatal closure patterns of the incisive suture were studied in 26 South African Plio-Pleistocene hominids (Table 1). Eleven of these are considered as *Australopithecus africanus* (Taung, Sts 5, Sts 17, Sts 52a, Sts 71, TM (Sts) 1512, Stw 73, Stw 391, MLD 6,

TABLE 1. List of the South African Plio-Pleistocene hominids studied with their estimated age at death

Specimen	Estimated age at death	Sources
Sts 5	Mature, same as Sts 6, (i.e., 35 \pm years)	Mann (1975)
Sts 17	21 \pm 2 years	Mann (1975)
Sts 52a	17 \pm 2 years (1); 11.3 years (2)	1) Mann (1975); 2) Bromage (1987)
Sts 71	33 \pm 2 years	Mann (1975)
Stw 53	Mature	
Stw 73	—	
Stw 252a, n, m	—	
Stw 391	—	
Taung	6½ \pm 1 years (1); 3 years (2)	1) Mann (1975); 2) Bromage (1985)
TM (Sts) 1512	21 \pm 2 years	Mann (1975)
MLD 6	20 \pm 1 years	Mann (1975)
MLD 9	Greater than 30 years	Mann (1975)
MLD 45	—	
TM 1517	20 \pm 1 years (1); approximately >10.5 years (2)	1) Mann (1975); 2) Bromage (1987)
Sk 12	33½ \pm 3 years	Mann (1975)
Sk 13	Adolescent (1); approximately 8.0 (2)	1) Mann (1975); 2) Bromage (1987)
Sk 46	34 \pm 3 years	Mann (1975)
Sk 47	13 \pm 2 years (1); 7.5 years (2)	1) Mann (1975); 2) Bromage (1987)
Sk 48	20 \pm 1 years	Mann (1975)
Sk 52	16 \pm 1 years (1); 11.3 years (2)	1) Mann (1975); 2) Bromage (1987)
Sk 79	32 \pm 2 years	Mann (1975)
SK 83	32 \pm 2 years	Mann (1975)
SK 847	34 \pm 3 years	Mann (1975)
SKX 162	Juvenile	
SKX 265	—	
SKW 11	Adult	

MLD 9 and MLD 45), 12 as *Australopithecus (Paranthropus) robustus* (Sk 12, Sk 13, Sk 46, Sk 47, Sk 48, Sk 52, Sk 79, Sk 83, Skw 11, Skx 162, Skx 265 and TM 1517a), and two as early *Homo* (Sk 847 and Stw 53). Clarke (1988) suggested that Stw 252, from Sterkfontein Member 4, with large teeth, represents a species ancestral to *A. (P.) robustus*.

A satisfactory picture of geographical variation (i.e., intraspecific variation) in pygmy and common chimpanzees was obtained by studying the skulls of 720 individuals of known geographical origin, from all allopatric species and subspecies: 123 *Pan troglodytes verus*, 223 *Pan troglodytes troglodytes*, 205 *Pan troglodytes schweinfurthi*, and 169 *Pan paniscus* combined into the following major geographic groups, except for *P. t. verus* (these latter specimens coming mainly from Liberia but representing different social groups).

P. t. troglodytes: group 1, left bank of the Sanaga river (Cameroon), between Yaoundé (03°52'N, 11°31'E), Sangmelima (02°56'N, 11°59'E), Kribi (02°56'N, 09°55'E), and Edea (03°47'N, 10°08'E), n = 107; group 2, south-east of Cameroon, between Doumé (04°15'N, 13°25'E), Batouri (04°26'N, 14°22'E), and Ouessou (01°38'N, 16°04'E), n = 78.

P. t. schweinfurthi: group 3, between the Uélé, Itimbiri, and Mangala rivers (Zaire), n = 49; group 4, between the Aruwimi and Elila rivers (Zaire), n = 89.

P. paniscus: group 5, between the Zaire, Lomela, and Lomani rivers (Zaire), n = 29; group 6, between the Zaire and Lomani rivers (Zaire), n = 116.

Ages and numbers of the specimens used in this study are listed in Table 2. Five age groups were distinguished: juvenile 1 (J1), defined as having exclusively an incomplete or complete deciduous dentition; juvenile 2 (J2), defined as not having second permanent molars; juvenile 3 (J3), defined as not having third molars; adult 1 (A1), defined as having a complete permanent dentition but incomplete closure of the spheno-occipital synchondrosis; and adult 2 (A2), defined as having a complete permanent dentition and a completely closed spheno-occipital synchondrosis.

In order to derive frequencies for the two bilateral components of the incisive suture, I divided the total number of times the trait occurred on either side by the number of sides on which the trait could be observed. Sex and age influence as well as differences between major geographic groups, subspecies, and species were tested with a Chi-square test with 2 \times 2 contingency tables (degree of freedom = 1). The following three categories of ectofacial sutural fusion were established to assess the degree of the incisive suture closure in its anterior and palatine portions: 1) no fusion (i.e., completely open), 2) incomplete fusion; 3) complete fusion.

RESULTS

The anterior component of the incisive suture

In younger specimens (J1), the anterior component is completely closed in more than four cases out of ten (41.3%) in *P. paniscus*

TABLE 2. Numbers, species, subspecies, age groups, and sex of the chimpanzee skulls studied

	Females					Males					Undetermined sex				
	J1	J2	J3	A1	A2	J1	J2	J3	A1	A2	J1	J2	J3	A1	A2
<i>P. t. verus</i>	2	3	4	12	23	2	2	5	12	38	2	2	1	3	12
<i>P. t. troglodytes</i>	8	14	12	16	66	7	11	16	8	26	5	5	6	3	20
<i>P. t. schweinfurthi</i>	5	12	8	3	19	6	10	8	9	24	9	19	11	16	46
<i>P. paniscus</i>	9	15	10	2	24	6	18	7	5	17	8	18	11	7	12

and in approximately one-tenth (8.3%) of cases in *P. troglodytes*. These frequencies increase regularly with age to occur in older specimens (A2) of *P. paniscus* and *P. troglodytes*, respectively, in more than nine and eight cases out of ten (respectively, 92.5% and 83.3%). Moreover, after birth, the anterior component of the incisive suture is never completely patent. Thus, its closure starts during fetal life. A complete closure occurs in the majority of specimens of *P. paniscus* and *P. troglodytes*, respectively, after the eruption of the first permanent molars (76.5%) and after the eruption of the third molars (50%), whereas the spheno-occipital synchondrosis is still patent. When Chi-square tests can be done, all the differences between *P. paniscus* and the three *P. troglodytes* subspecies are very significant (at $P < 0.05$) for all age categories, except in one case (Table 3). Thus, complete anterior closure clearly occurs earlier in *P. paniscus* (Fig. 3).

Comparisons of the anterior closure of the incisive suture within each chimpanzee species but either between major geographic groups or between subspecies give interesting information about geographical variation. No significant differences between groups 5 and 6, except in one case (Table 4), reveal geographical variation among pygmy chimpanzees. Moreover, no significant differences exist among either *P. t. troglodytes* (i.e., between groups 1 and 2) or *P. t. schweinfurthi* (i.e., between groups 3 and 4), except in one case (Table 4). I previously noted that the anterior closure pattern in *P. t. verus* is distinct from that of the other two currently recognized common chimpanzee subspecies (*P. t. troglodytes* and *P. t. schweinfurthi*) (Braga, 1995). Indeed, in *P. t. troglodytes* and *P. t. schweinfurthi*, the anterior component may be completely closed before the eruption of the second permanent molars (26.7% and 6.1%, respectively). In *P. t. verus*

the complete closure may occur only after the eruption of the third molars (27.8%). At this stage of development, in the other two subspecies, the complete anterior closure of the incisive suture occurs in *P. t. troglodytes* and *P. t. schweinfurthi* in 72.2% and in 50% of the specimens, respectively (Fig. 3). Thus, *P. t. verus* is clearly distinguishable by a later complete anterior closure of the incisive suture. In specimens with erupted third molars, the differences between *P. t. troglodytes* and *P. t. schweinfurthi* are either significant at the 2% level (A1) or not significant at all (A2). On the contrary, at this dental developmental stage, all the differences between the two former subspecies and *P. t. verus* are highly significant (Table 3). In *P. paniscus*, there is no significant influence of sex on the anterior closure of the incisive suture. In both *P. t. troglodytes* and *P. t. schweinfurthi*, only after the closure of the spheno-occipital synchondrosis is complete closure significantly more frequent in males than females. There is no side influence on the closure of this feature (Braga, 1995).

I have scored the degree of anterior closure of the incisive suture in fifteen specimens of Plio-Pleistocene hominids in which the anterior part of the face is preserved enough, especially its upper part (Table 5). Just as it does in chimpanzees, the anterior component starts to close at its lower part (i.e., near the alveolar border, margo alveolaris) in Plio-Pleistocene hominids. This is clearly visible on the youngest specimen studied, the Taung child. On the following five specimens, the anterior component of the incisive suture is incompletely closed: Taung, MLD 6, Sts 17, Stw 53, and MLD 45. Of these five specimens which partly exhibit the anterior component of the incisive suture, four are usually considered to be *A. africanus* (Taung, MLD 6, MLD 45, and Sts 17) and one an early *Homo* (Stw 53). One

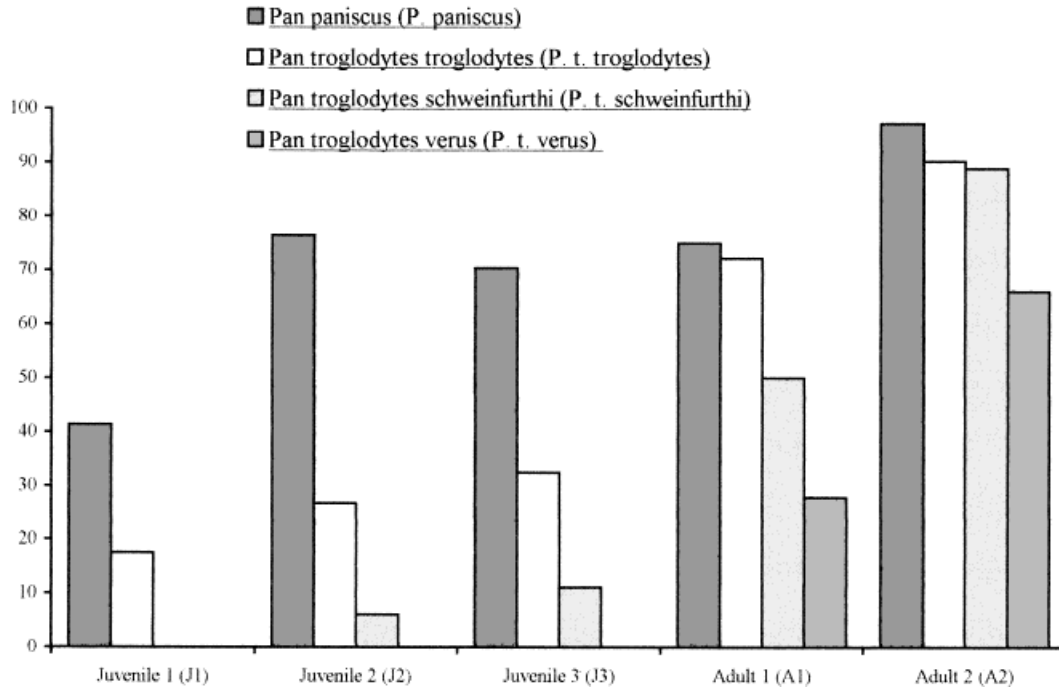


Fig. 3. Calculated frequencies for the complete anterior closure of the incisive suture in chimpanzees.

TABLE 4. Chi-square tests for differences either among pygmy chimpanzees or among the three common chimpanzee subspecies in the complete anterior closure of the incisive suture

	J1	J2	J3	A1	A2
Group 1 vs. group 2 (<i>P. t. troglodytes</i>)	.3355	.1892	.0720	.7306	.4551
Group 3 vs. group 4 (<i>P. t. schweinfurthi</i>)	*	.9761	.7871	.0000 ¹	.8939
Group 5 vs. group 6 (<i>P. t. paniscus</i>)	.7199	.5067	.0164 ¹	.8673	.7222

¹ Differences are significant (at $P < 0.05$).

* P cannot be calculated.

5 and 6, except in one case (Table 7). Moreover, no significant differences exist among either *P. t. schweinfurthi* (i.e., between groups 3 and 4) or *P. t. troglodytes* (i.e., between groups 1 and 2), except in one case (Table 7). In *P. t. verus*, the palatal closure, like the anterior closure, is distinguishable from that of the other two common chimpanzee subspecies. Whereas in the eastern subspecies, the palatal component may be completely open in specimens with only deciduous dentition, I never observed this trait in *P. t. verus* at the same developmental

state (Fig. 4). However, Chi-square tests reveal only significant differences between *P. t. verus* and *P. t. schweinfurthi* for the two first age categories (Table 6). No difference associated with sex was observed for the palatal component of the incisive suture.

In Plio-Pleistocene hominids, the degree of palatal closure of the incisive suture was scored on 21 specimens in which the palatal part of the face is preserved enough and, especially its medial part, close to the lower aperture of the incisive canal (Table 5). As in humans and chimpanzees, the palatal component starts to close in its lateral part (Fig. 2). On the Taung child, displaying erupted M^1 into occlusion but central incisors with little or no root formed yet, the palatal component is still completely open, on both sides, from the lower aperture of the incisive canal to the septum located between the lateral incisor and the canine. On the following nine specimens, the palatal component is incompletely closed: Sk 47, Sk 52, Sk 13, Skw 11, Sts 17, Sk 79, Stw 252a, Skx 265, Skx 162. In an *A. (P.) robustus* specimen, Skx 162, displaying unerupted crowns of

TABLE 5. Degree of anterior and palatal ectofacial closure of the incisive suture in South African Plio-Pleistocene hominids¹

Specimen	A.C.I.S.						P.C.I.S.						References	
	Right			Left			Right			Left			A.C.I.S.	P.C.I.S.
	a	b	c	a	b	c	a	b	c	a	b	c		
Sts 5	1	0	0	1	0	0	1	0	0	1	0	0	(2)	
Sts 17	?	?	?	0	1	0	0	1	0	0	1	0		
Sts 52a	1	0	0	1	0	0	1	0	0	1	0	0		
Sts 71	1	0	0	1	0	0	1	0	0	1	0	0		
Stw 53b	0	1	0	0	1	0	1	0	0	1	0	0	(4)	
Stw 73	?	?	?	?	?	?	1	0	0	1	0	0		
Stw 252a,n,m	1	0	0	1	0	0	?	?	?	0	1	0		
Stw 391	1 ²	0	0	?	?	?	1	0	0	?	?	?		
Taung	0	1	0	0	1	0	0	0	1	0	0	1	(2) (4) (5)	(2)
TM 1512	1	0	0	?	?	?	1	0	0	?	?	?		
TM 1517a	?	?	?	1	0	0	?	?	?	?	?	?		
Sk 12	1	0	0	1	0	0	1	0	0	1	0	0		
Sk 13	1 ²	0	0	1 ²	0	0	0	1	0	0	1	0		
Sk 46	1 ²	0	0	1 ²	0	0	1	0	0	1	0	0		
Sk 47	1 ²	0	0	?	?	?	0	1	0	0	1	0		
Sk 48	1	0	0	1	0	0	1	0	0	1	0	0		
Sk 52	1 ²	0	0	1 ²	0	0	0	1	0	0	1	0		
Sk 79	?	?	?	?	?	?	0	1	0	0	1	0		
Sk 83	1	0	0	1	0	0	1	0	0	1	0	0		
Sk 847	?	?	?	1	0	0	1	0	0	1	0	0		(3)
Skx 162	?	?	?	?	?	?	0	1	0	?	?	?		(6)
Skx 265	?	?	?	?	?	?	?	?	?	0	1	0		(6)
Skw 11	1	0	0	?	?	?	0	1	0	0	1	0		
Mld 6	0	1	0	?	?	?	?	?	?	?	?	?	(1) (4)	
Mld 9	?	?	?	?	?	?	1	0	0	?	?	?		
Mld 45	0	1	0	?	?	?	?	?	?	?	?	?		

¹ Two specimens (Sts 5, Sk 847) received different scores from this study and authors cited in references. A.C.I.S., anterior component of the incisive suture; P.C.I.S., palatal component of the incisive suture; a, complete fusion; b, incomplete fusion; c, no fusion (i.e., completely open); 0, absent; 1, present; ?, unpreserved. Numbers in parentheses correspond to the following references: 1) Dart, 1925; 2) Broom, 1946; 3) Robinson, 1953; 4) Clarke, 1985; 5) Bromage, 1985; 6) Grine, 1989.

² Only for the preserved part.

canines and premolars but erupted incisors and M¹, the palatal component is partially closed. In another specimen, TM (Sts) 1512, considered as an *A. africanus* representative, it is completely closed. In a younger putative *A. africanus* specimen, Sts 52a, the palatal component is also completely closed. Out of four *A. africanus* specimens showing a complete closure of the feature, three are adults (Sts 71, Sts 5, and MLD 9). In *A. (P.) robustus*, contrary to the pattern displayed by the anterior component, the palatal component of the incisive suture is partially closed in seven out of ten specimens. The younger one, Skx 162, displays erupted incisors and M¹. The three *A. (P.) robustus* specimens which show complete palatal closure (i.e., Sk 83, Sk 12, and Sk 46), are adults.

Anterior and palatal components of the incisive suture

In all chimpanzee taxa, the complete closure always occurs earlier for the anterior

than for the palatal component of the incisive suture (Fig. 5). In two *A. africanus* specimens in which both portions are recordable (Taung and Sts 17), the closure is more advanced for the anterior component than for the palatal component. The same pattern is expected in *A. (P.) robustus*. Indeed, in these specimens, while the anterior component is completely closed in two young specimens (Sk 48 and TM 1517a), the palatal component of the incisive suture is still partly visible in Sk 79, a much older specimen.

DISCUSSION

Previous interpretations of the relevance of the incisive suture to understanding hominid phylogeny

Wood-Jones (1929) interpreted early complete anterior closure of the incisive suture as "a distinguishing character of man as a species" to be used as a "specific diagnostic feature of *Homo*." Thus, we should ask when

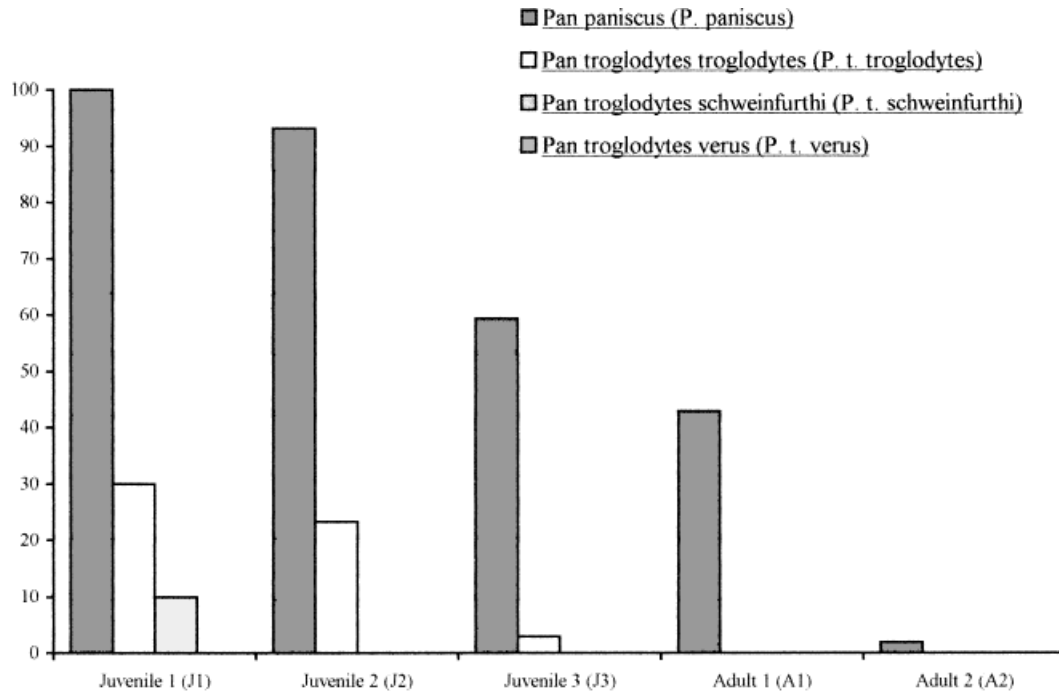


Fig. 4. Calculated frequencies for the complete palatal opening of the incisive suture in chimpanzees.

TABLE 6. Chi-square tests for taxonomic differences in the complete palatal opening of the incisive suture in chimpanzees

	<i>P. paniscus</i>					<i>P. t. verus</i>					<i>P. t. troglodytes</i>				
	J1	J2	J3	A1	A2	J1	J2	J3	A1	A2	J1	J2	J3	A1	A2
<i>P. t. verus</i>	.0000 ¹	.0000 ¹	.0000 ¹	.0000 ¹	.3489										
<i>P. t. troglodytes</i>	.0000 ¹	.0000 ¹	.0000 ¹	.0000 ¹	.1927	.8263	.6808	*	*	*					
<i>P. t. schweinfurthi</i>	.0000 ¹	.0000 ¹	.0000 ¹	.0000 ¹	.2689	.0494 ¹	.0000 ¹	*	*	*	.0504	.0000 ¹	.5803	*	*

¹ Differences are significant (at $P < 0.05$).

* P cannot be calculated.

TABLE 7. Chi-square tests for differences either among pygmy chimpanzees or among the three common chimpanzee subspecies in the complete palatal opening of the incisive suture

	J1	J2	J3	A1	A2
Group 1 vs. group 2 (<i>P. t. troglodytes</i>)	.0257 ¹	.3710	.6736	*	*
Group 3 vs. group 4 (<i>P. t. schweinfurthi</i>)	.6318	*	*	*	*
Group 5 vs. group 6 (<i>P. t. paniscus</i>)	*	.7552	.2807	.7462	.8004

¹ Differences are significant (at $P < 0.05$).

* P cannot be calculated.

early complete anterior closure of the incisive suture appeared during human evolution. With respect to early hominids, Wood Jones (1947:439) observed that "*Australopi-*

thecus and *Plesianthropus* show definite facial maxillary-premaxillary sutures in typical simian form." However, Wallace (1978: 288) considered that the "premaxilla was lost earlier in ontogeny in *Paranthropus* than in *Australopithecus* and *Homo*." Later, Clarke (1985) noted that the course of the incisive suture in the Taung child and in a craniofacial fragment from Makapansgat (MLD 6), though both specimens are considered to be *A. africanus* representatives, is different from the course of the feature seen in a facial fragment from Sterkfontein (Stw 53), which shows affinity to *H. habilis* (Hughes and Tobias, 1977). A careful study of the incisive suture closure in a large chimpanzee sample, representing all the

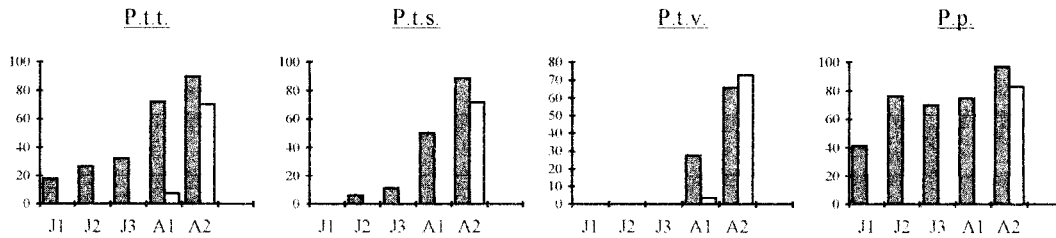


Fig. 5. Relative chronology of complete anterior and palatal closure of the incisive suture in chimpanzees. *P.t.t.*, *Pan troglodytes troglodytes*; *P.t.s.*, *Pan troglodytes schweinfurthi*; *P.t.v.*, *Pan troglodytes verus*; *P.p.*, *Pan paniscus*; J1, juvenile 1; J2, juvenile 2; J3, juvenile 3; A1, adult 1; A2, adult 2; dark, anterior component of the incisive suture; light, palatal component of the incisive suture.

currently recognized taxa, may facilitate understanding of the remarks of all of these authors, which span a period of more than 65 years. Furthermore, these original comparative data provide additional materials for interpreting growth patterns of early hominids. First we must make sure how these comparative anatomical data about the incisive suture closure parallel the molecular findings about chimpanzee polytypism.

Chimpanzee variation as revealed by the molecular data

Mitochondrial DNA results show that variation between the two chimpanzee species exceeds, by far, that within the common chimpanzee (Ruvolo et al., 1994). Moreover, analyses of chromosomes (Stanyon et al., 1986) and blood groups (Socha, 1984) reveal differences between the two species. Recently, Morin et al. (1994) found an "unexpectedly large genetic distance" between *P. t. verus* and the other two currently recognized common chimpanzee subspecies. Anatomically, two important differences arise, first between the two chimpanzee species and second among *P. troglodytes*. These anatomical differences give the same picture of chimpanzee polytypism as do the molecules. Between the two species of chimpanzees, two clearly distinct closure patterns of the incisive suture are noticeable. The complete anterior closure occurs significantly earlier in *P. paniscus*. Moreover, the complete palatal opening occurs in significantly higher proportions in *P. paniscus* than in *P. troglodytes*. Concerning the distinctiveness of *P. t. verus* among common chimpanzees, the closure patterns of the incisive suture paral-

els the findings using mitochondrial DNA analysis. As noted above, *P. t. verus* is clearly distinguishable from both *P. t. troglodytes* and *P. t. schweinfurthi* by a later complete anterior closure and an earlier palatal closure of the incisive suture. Geographical variation among either *P. paniscus*, *P. t. troglodytes*, or *P. t. schweinfurthi* is negligible. Moreover, sexual dimorphism does not play an important role in the incisive suture closure among chimpanzees (Braga, 1995). This knowledge of geographic, sexual, and interspecific variation in chimpanzees is fundamental to interpreting the incisive suture closure in early hominids. As results about the pattern of incisive suture closure in chimpanzees are consistent with the differences revealed by molecular data, I believe that chimpanzee variation provides a good comparative data set against which to interpret morphology among South African Plio-Pleistocene hominids.

Between species closure patterns of the incisive suture in Plio-Pleistocene hominids

Broom (1946) already emphasized a strong difference between the type specimens of *Plesianthropus transvaalensis* (Sts 5) and *Paranthropus robustus* (TM 1517a). However, though I was unable to observe even a small part of the anterior component of the incisive suture on Sts 5, Broom (1946) reported its presence. Yet a strong difference arises between *A. africanus* and *A. (P.) robustus* in the closure pattern of the anterior component of the incisive suture. Indeed, four *A. africanus* specimens (Taung, MLD 6, MLD 45, and Sts 17) exhibit a partially closed anterior component of the suture. In

contrast, all the *A. (P.) robustus* representatives exhibit a completely closed anterior component (Table 5), though two of them are supposed to be younger than the *A. africanus* specimens that exhibit this feature (Table 1). These results clearly indicate that the anterior closure occurs earlier in *A. (P.) robustus* than in *A. africanus*. Further discoveries of preserved young upper faces will permit the determination of whether it was completely closed at birth in *A. (P.) robustus*. However, from the data presented in this study, I conclude that in *A. (P.) robustus* as compared to *A. africanus*, complete anterior closure of the incisive suture is early in the same way that it is early for humans relative to birth and even the eruption of the first permanent molars. Indeed, this feature is never observed in infant human "skulls exceeding six years of age" (Ashley-Montagu, 1935), and complete closure occurs mostly during fetal life.

The phylogenetic relationships of the robust australopithecines are still unresolved. Moreover, data about early hominid anterior facial skeletons in which the incisive suture might be preserved and dated before 3 Myr BP are flimsy. The anterior component of the incisive suture is clearly seen on specimens from either Hadar (A.L. 333-86, a juvenile maxilla with unerupted I¹ and M¹ crowns; A.L. 333-105, a juvenile maxilla with unerupted right M¹ [Kimbel et al., 1982]) or Laetoli (LH-21a; a right maxilla with unerupted I¹, I², and M¹ [White, 1980]). However, in an adult specimen from Hadar (A.L. 333-1), there is no trace of this feature (Kimbel et al., 1982). Whether it occurs on another adult maxilla from Hadar has not yet been determined (A.L. 417-1d [Kimbel et al., 1994]). On the other hand, the later anterior closure of the incisive suture in *A. africanus* resembles the more primitive pattern in extant chimpanzees, the animals that in this study provide the outgroup comparison (i.e., extant chimpanzees reflect the ancestral condition [see Nelson, 1978]).

Ontogenetic significance

As noted above, in fetuses of both extant chimpanzees and humans, the incisive suture is patent, but, in humans with subsequent development, this suture closes completely during early life. Given this

ontogenetic character transformation, the presence of an anterior component after infancy is observed to be "more general" and its closure to be "less general" (Nelson, 1978). As regards the "state" of early closure, Wallace (1978:290) finds a "phylogenetic trend toward early loss of the premaxilla" during ontogeny. Thus, early complete anterior closure of the incisive suture during infancy, or even before, may represent the derived state and provides an additional feature in the already long list of similarities between robust australopithecines and early *Homo* (Kimbel et al., 1984; Dean, 1986; Skelton et al., 1986; Tobias, 1988, 1991; Bromage, 1992). Most of these are interpreted as homoplasies.

What is the developmental significance of both the earlier anterior closure (exposed in this study) and the peculiar course of the palatal component of the incisive suture (reported by Clarke, 1988) in *A. (P.) robustus*? An earlier anterior closure is the evidence for the absence of growth (bone apposition) in the contact area between the maxillary and incisive bones. This absence of growth is responsible for a reduced vertical and horizontal lengthening of the anterior face (Enlow, 1990) and a reduced lengthening of the incisivo-canine arch (Delaire, 1974). This phenomenon, associated with the "vertical hyperplasia of the posterior face," considered as "relatively extreme" in *A. (P.) robustus*, produces an "upward rotation of the nasomaxillary complex," as demonstrated by Bromage (1989:763). Moreover, McCollum (1994:270-271) considers that, in *A. (P.) robustus*, there is a "relative decrease in the degree to which the palatal lamina descends within the subnasal region" limiting "the extent to which the vomer can be displaced inferiorly within the nasomaxillary complex." The earlier anterior closure of the incisive suture in *A. (P.) robustus* may also be a consequence of this differential pattern of displacement. Is the earlier anterior closure accompanied, in *A. (P.) robustus*, by an earlier palatal closure of the incisive suture? My view is in the affirmative. Indeed, if two young specimens, Skx 162 and Taung, representing, respectively, *A. (P.) robustus* and *A. africanus*, are compared, the palatal closure is clearly more pronounced in Skx 162.

Two features should be associated with early anterior closure of the incisive suture in *A. (P.) robustus* as compared to *A. africanus*: the shortened upper precanine diastema and the distally rotated upper canines. Schultz (1948:178) found that the size of the upper diastema is "closely determined by the very variable, sagittal development of the premaxilla." Wallace (1978) found the width of the upper diastema to be higher in *A. africanus* (ranging from 1.2–2.4 mm, with an average of 1.7 mm) than in *A. (P.) robustus* (ranging from 0.2–1.7 mm., with an average of 0.7 mm). Either a small diastema or none may arise from an early closure of the incisive suture, while a longer growth period in combination with late fusion may produce the wide diastema seen in apes (Wallace, 1978). Interestingly, Wallace (1978) found distally rotated, permanent upper canines in robust australopithecines but not in *A. africanus* and considered this unique feature to be an adaptation to a shortened, compressed anterior arch. As compared to *A. africanus*, a reduced anteroposterior lengthening of the incisive bone in *A. (P.) robustus* (Clarke, 1988) is partly the consequence of an absence of growth at the palatal component of the incisive suture and, consequently, of an earlier closure of this suture. Inversely, an increasing area of incisive bone behind the incisors in *A. africanus* reflects increments of growth on the incisive side of the palatal component and thus a later closure of this suture. It is worth noting that the size of both the incisive bone and anterior teeth influence the incisive suture closure pattern (Ashley-Montagu, 1935). My finding on earlier closure of the anterior component of the incisive suture in *A. (P.) robustus* utterly confirm Clarke's (1988) observations of a dramatic reduction in anteroposterior dimension of the incisive bone in the robust form. Furthermore, the relatively small size of incisors and canines compared to the cheek teeth, which is a specialization of robust australopithecines, should have induced a reduction of the size of the incisive bone and consequently an early closure of both anterior and palatal components of the incisive suture. This hypothesis is still valid if we examine chimpanzee models. Indeed, Johanson (1974) found that all buccolingual and mesiodistal crown dimensions of the

upper deciduous and permanent incisors were very significantly smaller in *P. paniscus* than in *P. troglodytes* (at $P < 0.001$), while I found that the complete anterior closure of the incisive suture occurs early in pygmy chimpanzees. Finally, Dean (1988: 47) suggested that "the growth of the jaws and the space available for permanent teeth to emerge into the mouth" is associated with the eruption sequence of teeth. Therefore, the closure pattern of the incisive suture may be functionally associated with dental development, as suggested by Simpson et al. (1990).

Relative rates of development of permanent incisors and first molars are clearly distinct between humans and chimpanzees. At the time of emergence of the first molars (at 3–4 years of age in chimpanzees and 5–6 years of age in humans), human incisors (crowns and roots) are developmentally advanced compared to chimpanzees. Providing original data on dental eruption in common chimpanzees of known age and sex, Conroy and Mahoney (1991:253) confirmed that "the time lag between first molar and central incisor emergence in chimpanzees is about twice that of modern humans." Using high-resolution computed tomography (CT), Conroy and Vannier (1991a,b) demonstrated that *A. (P.) robustus* resembled humans in central incisor–first molar eruption, while *A. africanus* resembled the chimpanzee pattern. Later Conroy and Kuykendall (1995) concluded that the dental developmental pattern in *A. (P.) robustus* is "superhuman" and "unique" because it combines early development of both incisors (and other antemolar teeth) and molars. However, Bromage (1987) considered that the "human-like" dental development pattern of robust australopithecines existed "within an ape-like development period." In consideration of the major distinction in closure patterns of the incisive suture between humans and chimpanzees but also between *A. (P.) robustus* and *A. africanus*, Conroy and Vannier's findings (1991a,b) are very interesting. The closure patterns of the incisive suture may reflect the permanent incisor–first permanent molar emergence pattern, because the whole region in which incisors develop must be early stabilized before they erupt (Ashley-Montagu, 1935). This could explain why the

anterior closure of the incisive suture starts before incisor eruption in chimpanzees, which occurs about the same time as second permanent molar eruption. For the same reason, the advanced permanent incisor formation and eruption relative to the first permanent molar in robust australopithecines and humans, as compared to *A. africanus* and extant chimpanzees, should be closely associated with the early incisive suture closure.

Intraspecific variability of incisor suture patterns in Plio-Pleistocene hominids

Two distinct closure patterns of the anterior component of the incisive suture are observed among four *A. africanus* specimens of similar age (MLD 6, Sts 17, Sts 52a, and TM (Sts) 1512). While two of them plainly indicate a partially closed feature (MLD 6 and Sts 17), the other two individuals (Sts 52a and TM 1512) display a completely closed anterior component. If Mann's (1975) estimated ages at death are correct (Table 1), and the chimpanzee models defined in the present study are used, such a difference can be assigned to individual variation. However, if Bromage's (1987) estimation of age for Sts 52a is exact (Table 1), the two distinct closure patterns observed among this small *A. africanus* sample may be interpreted as interspecific variation. In this hypothesis, Sts 52a represents a distinct species of Sterkfontein Member 4 and exhibits a robust pattern in the anterior closure of the incisive suture. Rak (1985) and Kimbel and Rak (1993) set Sts 52a in the *A. africanus* hypodigm. So does Clarke (1988) in spite of his suggesting that the variation he observes within the Sterkfontein Member 4 *A. africanus* sample represents two species: *A. africanus* (including Sts 5, Sts 17, and Sts 52), with smaller teeth, and another hominid (including Stw 252, Sts 36 and Sts 71), with larger teeth. In his view the latter hominid may be ancestral to *Paranthropus*.

Further variability of the closure pattern of the incisive suture is observed in Stw 53, an adult specimen from Sterkfontein Member 5. This specimen, with heavily worn P³ to M² and moderate attrition on the M³, is considered to belong to the genus *Homo* (Hughes and Tobias, 1977). According to Clarke (1985), the course of the anterior

component of the incisive suture in Stw 53 suggests that, embryonically, maxillary bone had overgrown the premaxilla. However, among the 712 chimpanzee crania examined in this study, the anterior component of the incisive suture either passes along the lateral border of the pyriform aperture or enters superiorly into the pyriform aperture and emerges inferiorly near the nasopalveolar clivus. Often this is visible in younger specimens in which the anterior component is closed only in its lower half. This is also visible in *A. afarensis* (Kimbel et al., 1982). Moreover, if in Stw 53 bone from the maxillary ossification center spread anterior to the incisive bone, as in the human fetus, the result would be the complete anterior closure at birth from its upper to its lower course, as in human newborns. These data on embryology of the human incisive bone and its anterior relationship to the maxillary bone indicate that, in Stw 53, the incisive and maxillary bones unite by fusion at the ectofacial surface, as in chimpanzees, *A. afarensis* and *A. africanus*.

Others, focusing on different aspects of morphology than this study, have found that a supposed *H. habilis* from Olduvai (OH 62) was more similar to African apes than is *Australopithecus afarensis* (Hartwig-Scherer and Martin, 1991). This was regarded as problematic, because of known cranial resemblances between OH 62 and Stw 53, with the latter attributed to *H. habilis*. The problem, however is resolved if the present interpretation of the closure of the anterior component of the incisive suture in Stw 53 is correct. Though early *Homo* may have retained some ancestral conditions, as, for example, a later closure of the incisive suture, a much more probable explanation, from human embryological evidence, is that Stw 53 is not an early *Homo* representative. In my view, *A. africanus* and Stw 53 retain the primitive state for which *A. (P.) robustus* and all *Homo* representatives share the derived character state.

CONCLUSIONS

Providing comparative data for all chimpanzee species and subspecies, this study demonstrates that distinctive patterns of incisive suture closure characterize humans and chimpanzees. Furthermore, as results

about the incisive suture closure in chimpanzees are consistent with the differences revealed by molecular data, I believe that chimpanzee variation provides a good comparative data set against which to interpret morphology among South African Plio-Pleistocene hominids.

Two distinctive closure patterns of the incisive suture characterize *A. africanus* and *A. (P.) robustus*. I conclude that in *A. (P.) robustus* as compared to *A. africanus*, complete anterior closure of the incisive suture is early in the same way that it is early for humans relative to birth and even the eruption of the first permanent molars.

Finally, the later anterior closure of the incisive suture in *A. africanus* and Stw 53, a supposed early *Homo* from Sterkfontein Member 5, resembles the more primitive pattern in extant chimpanzees for which *A. (P.) robustus* and *Homo* share the derived character state. It is worth noting that the Taung child does not show the robust condition.

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